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Recent Progress in our Knowledge of the Development of the Ctenophora.

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IN accordance with my usual practice of making the Anniversary Address of the Linnean Society an exponent of recent progress in some department of zoological research, I have selected for the present occasion the additions which have of late years been made to our knowledge of the development of the Ctenophora.

In the summer of 1861 *Beroë ovata* made its appearance in great numbers in the Firth of Forth, and afforded me an opportunity of subjecting this beautiful Ctenophore to a careful anatomical and embryological study, and of making numerous drawings illustrative of its structure and development. Before, however, all the points I had wished to ascertain had been made out, the animals had disappeared from the coast; and in the hope of obtaining at a future period fresh subjects for examination, I contented myself with publishing an abstract without figures of the facts which I deemed most important, deferring the publication of the more detailed memoir to such time as I might be enabled to complete the unfinished observations. The opportunity, however, of doing so never occurred.

In this abstract * I called attention to the existence in the egg of an external structureless membrane, which is separated from the vitellus by a clear interval, while the vitellus itself previous to segmentation shows a differentiation into a denser peripheral layer and a central portion, which has the appearance of being composed of cells with clearer contents. The later observations of Chun go to show that this semblance to cells is only the expression of a vacuolated condition of the vitellus.

I pointed out that while the first stages of segmentation proceed in the usual way, the segmentation in its subsequent stages does not go on uniformly in all the previously formed cleavage-

* "Contributions to our Knowledge of the Structure and Development of the Beroidæ," Proc. Roy. Soc. Edinb. vol. iv. p. 519 (1862).

spheres, and that, in accordance with this, the segmenting ovum now presents spheres of unequal size. I showed that successive segmentation goes on with great activity in some of the spheres, while others continue unaffected by it, or present it with much less energy, and that the former become broken up into a multitude of cells, by which the latter become gradually enveloped, so that the ovum now presents two very distinct portions—a central one, composed of large spherical cells, and a peripheral one, of much smaller cells.

It was shown that on the completion of the peripheral layer a large lacunar cavity had become apparent among the cells in the centre of the ovum, and that soon after this a depression (the future mouth) takes place upon the surface of the embryo, and becomes deeper and deeper until the depression formed reaches the central lacuna, into which it finally opens. I overlooked, however, a still earlier stage, in which, according to Chun, the communication of the central cavity with the exterior takes place by means of an orifice, which shows itself at the pole opposite to that of the definitive mouth. To the embryo in this stage Chun assigns the significance of a *gastrula*, with its two embryonic leaflets, ectoderm and endoderm, its gastric cavity, and its mouth, which, however, has but a temporary existence, closing after a time, and being succeeded by the definitive mouth, which opens on the opposite pole.

I further showed that on the completion of the definitive mouth, the ocellus, with its capsule and the rudiments of the oval tentaculiferous disks (pole-plates), make their appearance on the aboral pole, and that the refractile corpuscles composing the ocellus may at this time be seen to be developed in the interior of special cells. The eight meridional rows of swimming-plates have by this time made their appearance, not at equal distances from one another, but in four pairs, extending from within a short distance of the aboral pole along the sides of the embryo, over about one fourth of the whole distance from pole to pole.

The next stage observed was characterized by the development of the vascular system. This commences by the differentiation of a portion of the large-celled tissue or endoderm, which constitutes the greater part of the embryo, into two somewhat pyriform masses, extending one on either side of the alimentary cavity, and which, simultaneously with their formation, become excavated by an extension of the central lacuna. They thus form two large

sacs appended to the central lacuna, and opening into it, and are to become the deep longitudinal or gastric vessels of the animal.

Nearly at the same time two other masses, exactly similar to the former, and also containing an extension of the central lacuna, are found opposite to one another on the two remaining sides of the alimentary cavity; so that this cavity is now surrounded by four sacs.

The two last-formed sacs now become divided, each into two, the halves diverging more and more widely from one another, and becoming more and more superficial, until we find them in contact with the peripheral or ectodermal layer of the embryo, each sac here corresponding to a pair of meridional swimming-bands and to the interval between them. The final dichotomy of the sacs now takes place, each of the last-mentioned dividing into two, from the peripheral towards the central side, leaving each half immediately under a meridional swimming-band; so that every swimming-band has now a sac to itself. The gradual conversion of the wide sac-like vessels into the narrow canals of the adult is easily understood. About this time the central cavity, into which the vessels whose development has been just described open, and which corresponds to the so-called funnel of the adult, has sent off two branches, which run towards the aboral pole, and form the canals which there open externally, one on each side of the sense-body.

Up to this point the embryo has been confined within the coverings of the egg; but in the stage next described the young *Beroë* was free. The meridional series of swimming-plates had extended further towards the mouth. The mouth was surrounded by a circular canal, into which the two deep longitudinal vessels (gastric vessels) had opened. The circular canal was probably developed from the oral extremities of these vessels as T-like branches, by whose inosculation the ring became completed. Four out of the eight meridional vessels (those, namely, which corresponded to the narrow sides of the stomach) had also opened into the circular canal; but the other four meridional vessels, though extending for some distance beyond the oral extremities of the series of swimming-plates to which they belonged, still terminated towards the mouth, each in a blind extremity. The eight meridional vessels had begun to send out their cæcal offsets, as yet few in number and simple. In a still further stage, the animal now

measuring about three fourths of an inch in length, all the meridional vessels had opened into the circular canal, while their cæcal offsets had become numerous and ramified. The series of swimming-plates, however, had not yet attained their entire length, while the generative organs had not made their appearance, and the processes which spring from the margin of the tentaculiferous disks were still nearly simple.

For reasons already mentioned this paper was unaccompanied by figures; and I have therefore probably no reason to complain that the points in which it anticipates the results of subsequent research have been either overlooked, as by Fol, who does not seem to have known of its existence, or to have been misunderstood, as by Kowalewsky, who, though aware of the existence of the paper, does not seem to have thought himself called upon to cite it. I am indebted to Alexander Agassiz first, and to Chun afterwards, for having amply recognized it.

Kowalewsky has studied the development of several species of Ctenophora, among which he has especially attended to that of *Eschscholtzia cordata*. His account of the structure of the egg in this Ctenophore agrees with my own in recognizing not only an external structureless membrane, but a differentiation of the vitellus into a peripheral and a central portion. The latter, however, he describes as composed of fat-globules; and he regards it as performing the function of a food-yolk (Nahrungsdotter), while the peripheral portion constitutes the formative yolk (Bildungsdotter), and affords the proper foundation for the embryo. With this view I am unable to agree. From my own observations, cited above, it follows that the whole mass of the ovum participates in the cleavage, and contributes directly to the formation of the embryo. Kowalewsky has seen the peripheral layer exhibit protoplasmic movements of contraction previously to the commencement of cleavage.

The remarkable and eminently characteristic feature in the egg-cleavage of the Ctenophora, which, as described above, results in an outer layer of minute cleavage-spheres, by which the central mass of larger, more slowly segmenting spheres becomes gradually enveloped, has also been well observed by Kowalewsky, who gives fuller details of the process than it was possible to embrace in the short abstract which I had myself published.

He describes the protoplasm of each of the large central spheres,

when these have been nearly enveloped by the layer of small peripheral spheres, as usually presenting towards its centre a more concentrated portion, in the form of a nucleus, from which filaments radiate towards the circumference of the sphere; but he does not regard this as representing a true cell-nucleus. He has noticed, however, a true cell-nucleus in each of the spheres composing the enveloping layer.

He has observed the formation of the swimming-plates, which he describes as originating in series of cells, which at first project hemispherically from the surface of the embryo. Each cell carries on its projecting end a set of fine hairs, which ultimately become fused together, and form the vibrating swimming-plate. Will, as cited by Chun, appears to have already noticed the formation of the swimming-plates out of cilia thus fused together.

The newest point in Kowalewsky's memoir is probably his account of the migration of cells from the surrounding parts into the gelatinous substance which is to constitute the great mass of the body in the adult. This jelly shows itself at first as a very thin stratum between the peripheral layer of cells and the central mass; and he believes it to be formed at the cost of the large central cleavage-spheres. It is at first perfectly clear and structureless; but as it increases in volume some of the cells of the peripheral layer detach themselves, and wander into the jelly. This migration of the cells becomes more and more active. The migrating cells at first project from the peripheral layer into the jelly, into which they send off pseudopodia-like prolongations, and finally completely detach themselves, and move into the deeper parts of the jelly, where their offshoots freely anastomose with one another. Treated with carmine solution, the homogeneous part of the jelly becomes coloured, while the cells which had migrated into it remain unaffected by the pigment.

The observations of Kowalewsky afford further evidence in favour of the nervous character of the ganglion-like body which lies under the so-called ocellus, with its capsule; for he finds filaments passing from it to be distributed to each of the series of swimming-plates, every plate receiving a small branch from the filament common to the entire series. The origin of the otolites each in a cell, from which they escape and reach the interior of the capsule, has also been noticed by him.

Kowalewsky has also followed *Cestum veneris* through some of the early stages of its development; and he finds that the seg-

mentation of the vitellus presents the features characteristic of all the Ctenophora hitherto examined. He has traced its development up to the formation of the series of swimming-plates, which he describes as composed, like those in *Eschscholtzia*, of confluent hairs. At this period the young Cestum has a globular form; and the tentacles are of considerable length, and are quite similar to those of *Eucharis*.

The development of *Eucharis multicornis*, of *Cydippe hormophora*, and of *Pleurobrachia* has also been studied by him; and, so far as his observations have gone, he finds the development of these Ctenophora to take place quite on the type of that of *Eschscholtzia*.

Kowalewsky has further examined the development of *Beroë Forskalii*; and, though he has but a slight acquaintance with my own published researches on the development of *Beroë ovata*, he confirms, in their essential features, most of the results to which I had already arrived.

Some observations on the development of the Ctenophora have also been made by Fol, and published by him in the form of an inaugural dissertation *.

He describes the structure of the egg in *Euramphæa vexillifera*, Gegenb., his account of which agrees in all essential points with the previously published descriptions of the egg of other Ctenophores. He has observed also the phenomena of segmentation, and has seen the formation of both the large and the small segment-spheres, and the envelopment of the former by the latter. He appears to have seen the differentiation of the four endodermal masses which are to become the primordial trunks of the vascular system; but he does not seem to recognize their significance; while his account of the formation of the digestive cavity and funnel is but fragmentary, and, judging from the analogy of other species, is less in accordance with the actual course of the development than are the descriptions which had been previously published. His account of the proper embryonal development does not go beyond this stage; and the few further details which he gives us, apply to the young Ctenophore in a much more advanced stage of growth.

* Hermann Fol, 'Ein Beitrag zur Anatomie und Entwickelungsgeschichte einiger Rippenquallen,' Berlin, 1869.

Fol's dissertation, however, is mainly occupied with an account of the anatomy of adult forms; and the memoir is throughout illustrated by well-executed figures of development and structure.

The series of researches which, next in point of time, has contributed most to our knowledge of the development of the Ctenophora, we owe to Alexander Agassiz, who has given us a well-illustrated and valuable memoir on the embryology of *Idyia* (*Beroë*) and of *Pleurobrachia* *. In his account of the structure of the egg and of its development, he has confirmed in most points the results obtained by Kowalewsky, Fol, and myself, demonstrating by independent observation the remarkable process by which the first formed cleavage-spheres become gradually enveloped by a layer of smaller spheres resulting from a later division of those previously formed †.

He has studied in great detail this process, and describes the eight segment-spheres first formed as arranging themselves round

* Alexander Agassiz, "Embyology of the Ctenophora," Mem. of American Acad. of Arts and Science, vol. x. 1874.

† It may be a question how far the enveloping layer of small spheres represents a continuation of the proper yolk-cleavage, or is to be regarded as a post-morular formation. Agassiz, if I have correctly interpreted his remarks, would seem to maintain the latter view; and with this I am disposed to agree, though it is difficult to say where in the Ctenophora yolk-cleavage ends and a proper organ-formation begins, or what stage in the development of the egg we are to consider as corresponding to the proper mulberry-like condition of other ova. If we regard the proper yolk-cleavage as coinciding with the division of the egg-cell only so long as this continues uniform, we shall have a definite character to rest on, and the formation of the small peripheral spheres will then be a post-morular phenomenon resulting in the formation of the two germinal layers, ectoderm and endoderm. The mulberry-like condition would, it is true, in accordance with this view be completed at a much earlier stage, and be represented by a much smaller number of cells than perhaps in any other ascertained instance; but, notwithstanding this, the whole process could be brought more into accordance with what we already know of yolk-cleavage and its immediate results than would be possible if we were to regard the formation of the small peripheral spheres as a direct continuation of the proper yolk-cleavage.

The formation of the peripheral layer of small dark spheres by which the central large clear spheres become enveloped results in a condition which must be carefully distinguished from that of the unsegmented ovum, in which we have also a central clearer mass surrounded by a peripheral darker layer.

a vertical axis, while from that end of each which is turned towards the "actinal" pole of the ovum, or the pole where the mouth is ultimately to show itself, a small segment becomes constricted off. In the eight small spheres thus resulting, segmentation now sets in with great activity; these spheres multiply rapidly by division; and it is the layer of cells so formed which gradually extends towards the opposite pole of the egg over what remains of the eight large spheres, until these are finally completely enveloped by it. The large spheres also become multiplied by division, but much more slowly than the small ones.

The enveloping layer thus formed he calls the embryonal layer, and regards it as that from which the embryo is directly developed, while he regards the included spheres as performing only the functions of a food-yolk. This view, however, I find it as difficult to bring into harmony with my own observations cited above as I do the somewhat different views of Kowalewsky regarding a formative and a food-yolk *. It appeared to me certain that the mass of central spheres is the source from which the whole vascular system of *Beroë* is directly developed †. Indeed this, as has been since especially insisted on by Chun, is to become the endoderm, while the peripheral layer is the foundation of the ectoderm.

Agassiz has also seen the commencement of the swimming-plates in local accumulations of the cells which constitute the outer layer, and has recognized the formation of the mouth in a depression which takes place in a thickening of this layer at one pole, while the sense-body originates in a similar thickening at the opposite pole. He has further followed the formation of the digestive cavity, which shows itself as a deepening of the oral depression, accompanied by an inversion of the outer layer, the inbulging thus formed being described as gradually extending through the axis until it reaches the walls of the embryo at the opposite pole. He does not appear, however, sufficiently to insist on the fact that the tube formed by the inversion of the superficial layer always opens into a cavity which had been already formed in the centre of the embryo. I regard the independent formation of this central lacuna, and the opening into it of the digestive canal, as one of the most important morphological facts in the embryology of the Ctenophora.

* See above, p. 92. † See above, p. 91.

The interesting observations of Kowalewsky regarding the formation of the gelatinous tissue have been confirmed by Agassiz, who has seen this tissue pervaded by cells, which have detached themselves from the outer walls, and migrated into the gelatinous mass.

The vessels are described as originating in four outbulgings of the digestive cavity, which rapidly push their way towards the oral pole. These tubes, as pointed out in the abstract cited above (see p. 91), really result from the transformation of the four great endodermal sacs, whose cavities are continued from the central cavity of the embryo, which ought to be distinguished from the true digestive cavity, being the part which is to become the so-called funnel of the adult.

Agassiz had already described * some of the more important stages in the post-embryonal development of *Pleurobrachia* (Cydipidæ) and of *Mertensia*, as well as in that of *Bolina*, which may be taken as a typical example of the lobate group of the Ctenophora, and had illustrated his memoir with many beautiful and highly expressive woodcuts. In the present memoir he has made a very careful study of the entire embryology of *Pleurobrachia*, and has shown that, setting aside the formation of the long retractile tentacles, which are absent in *Beroë*, it is in all points almost identical with that of *Beroë*. He has also shown that the changes undergone by the young *Mertensia* during its post-embryonal development, have an almost complete identity in all essential points with the post-embryonal changes of *Pleurobrachia*.

While the changes of *Beroë*, *Pleurobrachia*, and *Mertensia* during their post-embryonal development are not by any means striking, those presented by *Bolina* are on the contrary shown to be very great—a fact to which, in some important points, MacCrady had already, as cited by Agassiz, called attention. Up to the time when the young *Bolina* is ready to escape from the egg it can scarcely be distinguished from *Pleurobrachia* during a corresponding period, except in the fact that the compression of its body is in a plane at right angles to that of the compression in *Pleurobrachia*. It is after this that we find those well-marked changes of form, which show themselves in the acquisition of

* Alex. Agassiz, in Illustr. Catal. of Museum of Comp. Zool. Harvard College, 1865.

auricles and lobes, the complex windings and anastomoses in these of the vessels, and the almost complete disappearance of the tentacles, at first highly developed, like those of *Pleurobrachia*, changes which result in the very different and remarkable form of the adult *Bolina*, with its great lobe-like appendages and auricles.

By far the most elaborate and important treatise which has yet appeared on the Ctenophora is the recent great work of Chun on the 'Ctenophora of the Bay of Naples'*. This finely illustrated work is one of the many valuable contributions to zoology which we owe to the opportunity of research afforded by the Zoological Station at Naples. It treats of all the principal Ctenophoral groups, in their anatomical, embryological, and systematic relations.

His study of the development of *Eucharis multicornis* is made by Chun the basis of his general account of Ctenophoral embryology. To the two portions of the egg, the peripheral and the central, to which attention has been already called, he applies the terms "ectoplasm" and "endoplasm." The former he describes as a proper albumen-holding protoplasm, and the latter as a clearer vacuolated "cell-sap," and refers its apparent constitution out of spheres to its vacuolated condition.

The nucleus, which had escaped detection by the earlier observers, has been found by Chun imbedded in the ectoplasm. Kowalewsky†, though he failed at first to find it, recognized it afterwards in *Eschscholtzia* and *Eucharis*, while Hertwig‡ had seen it in *Callianira* and *Beroë*. Chun now finds it in all the Ctenophora examined by him.

The egg-cleavage is fully described; and in his account of its general character he confirms most of the observations made by Agassiz, Fol, Kowalewsky, and myself, while he adds some de-

* Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Herausgegeben von der zoologischen Station zu Neapel. I. Monographie. Ctenophora von Dr. Carl Chun. Leipzig, 1880.

† A. Kowalewsky, Investigations on the Development of the Cœlenterata, with 8 plates, in the Transactions of the Imperial Society of the Friends of Natural History, Anthropology, and Ethnography, Moscow 1873. This memoir is unfortunately published in the Russian language, and I am acquainted with it only through an abstract in Hoffmann and Schwalbe's 'Jahresberichte der Anatomie und Physiologie,' 1873.

‡ "Ueber den Bau der Ctenophoren," Jenaische Zeitsch. f. Naturwiss. Band xiv. p. 313 (1880).

tails regarding the later stages of this process. After the cleavage has advanced to the formation of four equal spheres lying in one plane, the next cleavage intersects the four spheres in an oblique direction, and divides each of them into a larger sphere, and a smaller one which lies obliquely upon it. The eight spheres, now no longer lying in the same plane, present a further difference in the fact that the main mass of the granular ectoplasm has passed over to the four small superjacent spheres, clothing them with a thick layer, and rendering their colour darker than that of the others—a condition which I had not noticed in *Beroë*, where, as Chun admits, it is by no means obvious.

As a general rule the eight segment-spheres thus formed divide almost simultaneously, each into two of dissimilar size. In this process nearly the whole of the ectoplasm is carried over into the eight smaller superjacent cells, while the eight large cells on which these lie consist chiefly of the endoplasm, being overlain only by a thin, scarcely visible layer of ectoplasm. In the later stages the endoplasm collects more and more about the nucleus of the large clear spheres, while their vacuoles flow together into a continuous cavity traversed by irregularly radiating and branching filaments from the central endoplasm.

After the cleavage has thus advanced so far that eight small cells lie on the eight larger ones, the first begin very suddenly and with great activity to divide, while the others remain quiescent. In *Lampetia* alone, which presents in its development many peculiarities, do we find the division of the large cells going on at the same rate with that of the small.

By the energetic division of the small cells the mass formed by the subjacent eight large cells becomes surrounded by a ring-like mantle, which gradually extends towards the poles. In the meantime division has been resumed in the subjacent cells, which from eight have become sixteen; and by the centrifugal separation of these cells from one another in the centre of the mass there is here formed a large vacuolar cavity which extends through the entire axis of the embryo. The enveloping cell-layer continuing to advance towards the poles, one of these becomes soon closed in, while the opposite pole remains as yet uncovered. About this time division is once more repeated in the sixteen large cells, without, however, presenting the regularity which had hitherto characterized this process.

In the stage at which the embryo has now arrived, with its two

layers of cells and its central cavity, and with one pole closed while the opposite pole remains open, Chun has recognized the morphological significance of a gastrula, and sees in the two layers of cells which form its walls the two primitive germinal layers, ectoderm and endoderm. He thus takes a view very different from that of Kowalewsky and A. Agassiz, who regard the large central cells as having the physiological value of a food-yolk. My own observations on the development of *Beroë*, as cited above, lead me to conclusions quite in accordance with the view taken by Chun.

The central cavity still communicates with the exterior by the gastrula-mouth, but becomes narrower by the pressure exerted by the ectoderm-cells, and is at last reduced to the condition of a narrow slit. In the meantime the ectoderm layer has been extending itself concentrically over the open pole, which it finally completely covers, and thus permanently closes the gastrula-mouth.

After the ectoderm has in this way completely grown over the endodermal cells, and both the poles have become closed, a thickening of the ectoderm may be noticed on each pole, caused on that where the gastrula-mouth had been situated by the cells here acquiring an elongated cylinder shape, while on the opposite pole the thickening is the result of the multiplication of the cells, which here become disposed in several layers. Out of the elongated ectoderm-cells which have shown themselves on the pole previously occupied by the gastrula-mouth, the central nervous system is to be differentiated, while in the thickened ectoderm of the opposite pole an inbulging may now be noticed; and we thus obtain the definitive mouth and the foundation of the digestive canal.

With this stage we have the first data for the orientation of the embryo; for we can now distinguish an oral pole from the opposite sense-pole, the axis passing through the two poles being the main axis of the Ctenophore.

Simultaneously with the accumulation of ectoderm-cells on the oral pole a similar accumulation may be seen in all Ctenophores, except the Beroidæ, on the right and left half of the embryo. The paired protuberances thus formed represent the foundation of the tentacle-apparatus.

Very early four symmetrically placed groups of ectoderm-cells become differentiated in a meridional direction from the rest by

enlarging and assuming a cylindrical form. Upon some of these cells may soon be seen a number of exceedingly fine cilia, which almost at their first appearance unite with one another, and form the embryo swimming-plate, as first observed by Will and afterwards by Kowalewsky. Each swimming-plate is thus the produce of a single cell.

Chun was the first to call attention to the fact that the entire ectoderm of the embryo is clothed with exceedingly minute vibratile cilia. Of these cilia eight linear series become more strongly developed simultaneously with the appearance of the swimming-plates, extend from the aboral end of every swimming-plate series towards the sense-pole, unite two by two, and finally end in the base of four strong sabre-shaped oscillating cilia.

When the ectodermal layer has closed over the gastrula-mouth, the cells composing it here multiply by division over a small polar area, and at the same time become elongated to about twice their original height. The sharply circumscribed ectoderm-region thus formed becomes somewhat rounded, sinks a little below the surface, and forms the central nervous system. Two semicircular groups of ectoderm-cells may now be seen, one on each side of the central nervous system. These soon acquire an elongated oval form, with the long axis in the plane of the stomach, and become the "pole plates." Surrounding the central nervous system may now be seen four groups of strong cilia. These increase in height, unite with one another so as to form a closed cilia-wreath round the nerve-mass; and finally the individual cilia become fused together and arch over the nerve-mass in the form of a closed capsule.

At an early period strongly refringent corpuscles may be noticed in many of the nerve-cells. These are finally expelled from their generating cells and become agglomerated into an otolite-heap, which lies in the interior of the nerve-capsule, where it is driven from place to place by the action of the cilia, which line the floor of the capsule, until it finally adheres to the curved ends of the four large sabre-shaped cilia already mentioned. The otolites are composed of phosphate of lime.

The central nervous system thus, of all organs of the Ctenophora, attains earliest its definitive form. Through its intimate relation to the swimming-plates it is among the most characteristic organs of the Ctenophora, and is found in all the species with great uniformity.

At the pole opposite to that where the gastrula-mouth had been situated, and which is now occupied by the site of the central nervous system, an inbulging of the ectoderm may be seen to take place in the line of the main axis. This gives us the origin of the definitive mouth and of the stomach, which continues to force its way deeper and deeper until it reaches a point a little beyond the middle of the body, and soon opens into the cavity which from a very early period had existed in the interior of the embryo, and which now becomes widened towards the sense-pole, and forms the foundation of the funnel. Even at this early period the lateral compression of both stomach and funnel may be seen, the two planes being placed at right angles to one another.

In the meantime the endoderm had become divided into two halves separated from one another by the plane of the stomach, and each of these again into two halves separated by the funnel-plane. Into each of the four endodermal masses thus differentiated an offset from the funnel extends, gradually advancing towards the mouth-pole, and soon widening into a considerable lumen. In these four sac-like masses of endoderm we have the first traces of the vascular system.

Between the stomach, funnel, endodermal sacs, and ectoderm the gelatinous tissue had already begun to be secreted as a clear layer, into which Chun had seen the migration of the richly ramifying cells from the ectoderm and stomach, to which Kowalewsky and Agassiz had already drawn attention. By the continued secretion of the jelly the embryo increases greatly in volume, and the endoderm-sacs become very distinct.

It is in the stage just described that, according to Chun, most embryos leave the egg, after which the differentiation of the definitive vascular apparatus out of the endoderm-sacs takes place. In *Beroë*, however, I have found development proceeding within the egg to a much more advanced stage.

Chun here makes an important generalization which legitimately follows from the course of the development now traced—namely, that two cavities destined to play different physiological parts in the life of the animal, one being devoted to the digestion of the nutriment and the other to its distribution, are derived respectively from two different germinal layers. The stomach owes its origin to the ectoderm, being formed by an in-

bulging of this membrane; while the funnel and the vessels which proceed from it are formed out of the large-celled endodermal tissue. This view, which is quite in accordance with my own observations (see above, p. 91), is inconsistent with the opinion that the large clear central cells serve only as a food-yolk.

The further, or post-embryonal development of the Ctenophora —that which takes place after their exit from the egg—does not offer the same uniformity as that found in the stages hitherto traced; and Chun describes it as it presents itself in different groups. He takes *Eucharis multicornis*, which had already afforded him a type for his description of the earlier stages of Ctenophoral development, as a type also of the post-embryonal development of the lobed Ctenophora.

When *Eucharis multicornis* leaves the egg it is of a pyriform figure and laterally compressed, so that the axis in the plane of the funnel exceeds in length the axis in the plane of the stomach. This is the characteristic condition of the *adult* state of another Ctenophoral genus, *Mertensia*, and is in striking contrast with the adult form of *Eucharis*, in which the axis in the stomach-plane is longer than that in the funnel-plane.

The tentacular apparatus lies concealed in small sheath-like depressions of the surface, one on either side. Each sheath contains two short rudimentary tentacles, of which the upper one rapidly grows and develops lateral branches, while the lower one remains rudimentary. The central nervous system is surrounded and overtopped by four roundish prominences of the gelatinous tissue. The ribs consist each of from four to five swimming-plates. The cells which had migrated into the jelly from the ectoderm and stomach-walls have already become elongated into true muscle-cells, and show themselves as fibres lying between the gastrovascular apparatus and the periphery.

Hitherto the vascular system has not shown an obvious distinction into funnel, central, and peripheral portions, and consists merely of two sacs which communicate with the central lacuna and send out short bulgings towards the ribs and the tentacular apparatus. The next changes, however, are essentially marked by the increased differentiation of the vascular system. Chun describes the two vessels which run along the broad side of the stomach towards the mouth (Magengefässe) as originating in ampuliform outbulgings of the two endodermal sacs; and though

he takes the same view of the origin of these vessels in *Beroë*, this does not correspond with the result of my own observations, from which I felt justified in concluding that in *Beroë* the two vessels in question originate in a direct transformation of two of the four sac-like masses which are differentiated out of the cells of the endoderm.

The larva increases in size; the stomach tapers from the wide mouth towards the laterally compressed funnel into which it opens. From the funnel the vessels are seen to be given off; and their regular dichotomous distribution, which is so characteristic of the Ctenophora, has begun to show itself. The four prominences which had raised themselves round the central nervous system have disappeared; and this lies henceforth free on the summit of the aboral pole.

The next development-stage of *Eucharis* is characterized by the appearance of the lobes, and by the unequal growth in length of the meridional vessels. The lobes show themselves as two lateral projections lying in the funnel-plane. At the same time a difference in the length of the meridional vessels becomes manifest, the four "subventral" vessels exceeding in length the four "subtentacular."

All the meridional vessels now grow rapidly towards the mouth-margin, extending themselves along the outer side of the lobes. When arrived at the oral region of the body, they begin to bend round on each side towards one another, and the subtentacular vessels anastomose with the subventral. The difference in length between the stomach-axis and the funnel-axis has now almost entirely disappeared, and the compressed *Mertensia*-like form of the larva has given place to a nearly spherical form.

To this stage of development would seem to succeed a remarkable form, which, though Chun did not trace it by continuous observation directly from the *Eucharis*-larva, having only obtained it in the towing-net, he believes, nevertheless, to be one of the forms which enter into the post-embryonal metamorphosis of *Eucharis*. The distribution of the vessels corresponds to that of the stage just described; but it is the only Ctenophore in which the main axis, or that which passes from the oral to the aboral pole, is much exceeded in length by the two lateral axes. This, along with the considerable development of the lobes, gives it a medusa-like aspect. Now, too, for the first time in the development-cycle of *Eucharis* do we find the plane of compression of

the animal corresponding to that of the adult; for we have the stomach-axis now exceeding in length the funnel-axis.

A further remarkable fact has been noted by Chun in this medusa-like larva, namely the total disappearance of the tentacle and the atrophy of the vessel which had supplied it; while at a later stage an entirely new tentacular apparatus becomes developed, and remains as the definitive tentacular apparatus of the *Eucharis*.

The central nervous system lies quite free on the aboral pole. Within the bell-like capsule may be seen the heap of otolites borne by the four large curved cilia, in which the lines of minute cilia which run along the course of the nerves terminate. The pole-plates have acquired their elliptical form; and on the sides of these the funnel-canals open with wide excretory orifices. The eight nerves run each to a swimming-plate series, extending through the entire length of the series, and communicating with every swimming-plate. At some distance from the last plates of the subtentacular ribs may be seen a number of minute plates, which are kept in connexion with the subtentacular ribs by a line of cilia. In these four rather isolated series of minute swimming-plates we see the foundation of the four so-called auricles, which, along with the lobes, are characteristic of the lobate section of the Ctenophora. The continuation of the nerve which runs along the rib may be also followed along the rudimentary auricles.

In the later stages the body becomes much elongated in the direction of the main axis, and the four gelatinous prominences become developed on the aboral pole round the central nervous system. At the same time the anastomosing meridional vessels have become thrown into complicated windings on the lobes, and the two stomach-vessels finally enter into the anastomosis.

A peculiarity of structure, which seems to have escaped the earlier observers, has been noticed by Chun in *Eucharis*. This consists in a blind sac, which, in the young animal, begins to show itself over the tentacle-basis in each body-half. It thence extends obliquely towards the stomach; and when arrived in the proximity of the stomach, it extends with the further growth of the animal in a direction chiefly towards the sense-pole and parallel to the stomach-walls, until in fully developed animals it reaches the funnel, or may even extend beyond it. Chun is unable to throw any light on the morphological significance or

physiological role of the blind sacs, no trace of which has been found in any of the other lobed Ctenophora*.

Among the most valuable observations of Chun are those which he has made on the development of *Cestum*, and which, with the exception of some fragmentary observations of Kowalewsky, afford almost the only information we possess regarding the embryology of this most interesting and highly aberrant type of Ctenophora. Chun has succeeded not only in observing the just hatched larva of *Cestum veneris*, but in following almost continuously its metamorphosis.

Cestum, when just hatched, presents the *Mertensia* type of form, and is almost identical in shape with the young *Eucharis*-larva, the difference between the two being found mainly in the tentacles, each of whose lateral filaments carry in the *Cestum*-larva a terminal knob of peculiar prehensile cells (Greifzellen). Each rib carries from four to five swimming-plates.

The *Mertensia*-like compression of the body is very obvious, the diameter in the plane of the funnel considerably exceeding that in the plane of the stomach; and this is rendered all the more significant when we bear in mind that in the adult not only is the compression of the body the reverse of this, but the length of the stomach-axis in the great band-shaped Venus's Girdle may be even a hundred times greater than that of the funnel-axis. Chun here remarks, with justice, that in few groups of the animal kingdom does the post-embryonal metamorphosis so strikingly recapitulate, even in the details of organization, the adult forms of more simply organized groups, as do the larval states of *Cestum* and the lobed Ctenophora recapitulate the configuration of the adult *Mertensiæ*.

The gastrovascular system shows, as yet, no obvious difference between central and peripheral vessel-trunks; but as the larva increases in size we find the vessels rapidly assuming their definitive distribution, and presenting a dichotomy so regular and normal that Chun has taken the *Cestum*-larva as an illustrative example of the typical form of the distribution of the vessels in the Ctenophora.

* We cannot avoid being here reminded of very similar sacs in certain Polyzoa, as well as of the segmental organs of the Annelida. It would be rash, however, to push the comparison further, and insist on a homological relation between the blind sacs of *Eucharis* and the segmental organs of the Annelida.

The tentacular apparatus, which is situated on a level with the funnel, gives origin not only to the main tentacle-stem with its lateral filaments, but also to a small independent stem, which Chun speaks of as a "reserve tentacle."

The condition of the ribs is very interesting in relation to the changes of form of the larva. By the time that the vascular system has nearly attained its characteristic dichotomous division, the four or five swimming-plates with which each rib had been hitherto provided have become reduced to a single one, to which a nerve runs from the central nervous system. In this change that plate which in each rib lies nearest to the sense-pole has become greatly increased in breadth, while those which follow it become atrophied and finally disappear.

The *Mertensia*-like flattening of the body in the plane of the stomach now gradually disappears, and the larva appears circular in transverse section. Soon, however, it presents again a slight flattening; but this is in the plane of the funnel, and with the growth of the larva becomes more and more decided, the length of the stomach-axis exceeding more and more that of the funnel-axis, until finally the long band-like form, characteristic of the adult Venus's Girdle, is attained.

With the band-like extension of the body the "subventral" meridional vessels are drawn out in the same direction, while the stomach-vessels send off each on the mouth-margin two branches at right angles to the main trunk, and the "subtentacular" vessels also diverge more and more to the right and left. At the same time the tentacular apparatus undergoes certain important changes. While the main tentacle still retains its original form, finger-like processes bud forth from the reserve tentacle: those at the proximal part of the tentacle remain fused together; but at the distal end they are differentiated into separate independent processes.

Though Chun has not succeeded in observing all the stages of the development of the tentacular apparatus, he regards it as almost certain that it is this reserve tentacle which is ultimately to become the definitive tentacle of *Cestum*.

Along the course of the subventral vessels new swimming-plates now make their appearance. Though at first arranged nearly vertically, this disposition rapidly yields to a horizontal one as the animal continues to assume its definitive band-like form. The form of the animal is now nearly that of a rectangle;

and the subventral vessels present a nearly horizontal direction in the greater part of their course, and then bend down in a vertical direction towards the oral edge of the rectangle; and as the swimming-plates are confined to the horizontal portion, the direction of each series is that which we meet with in the adult.

In the larva we can now plainly distinguish an aboral edge furnished with swimming-plates, an oral, and two lateral edges. On the latter the vertical ends of the subventral vessels run downwards towards the oral edge, while along this edge the horizontal branches of the stomach-vessels continue to extend themselves towards the angle formed by the meeting of the lateral and oral edges. Here they meet the ends of the subventral vessels, and anastomose with them. Each of the subtentacular vessels also extends in an oblique direction, from its origin under a subtentacular rib which never carries at this time more than a single swimming-plate, towards the same angle, where it meets the other vessels and soon enters into the anastomosis. The course of the vessels which characterizes the adult *Cestum* is thus in all its essential features established.

The body continues to elongate itself more and more in the form of a band; and with the consequent extension of the subventral vessels and their ribs numerous new swimming-plates are developed on the latter, while a few also show themselves on the subtentacular ribs, and the place of communication between the meridional vessels and the horizontal branches of the stomach-vessels moves towards the middle point of the lateral edges.

In the meantime the tentacle-apparatus has begun gradually to sink towards the mouth; and its sheath, appearing as a duplication of the dermal layer of the body, extends more and more over the tentacle, and runs on the margin into two furrows—the later tentacle-furrows. The original tentacle-stem with its accessory branches is still visible on the sheath; but at a later stage there is no longer any trace of it, and its place is taken by a tentacle-stem formed of numerous coalesced filaments, of whose origin from the reserve tentacle Chun believes there can be no doubt.

Chun also devotes some pages to a description of the post-embryonal development of the Beroidæ. Under this, however, he includes many stages which, in the examples examined by myself, were completed before the escape of the animal from the egg. The difference may depend on a difference in the species or

in external conditions, but is of no importance in the present inquiry.

In his account of the changes undergone by *Beroë* in the course of its development, Chun is not quite in accordance with some of the results at which my own observations led me to arrive. After the four endodermal sacs have been differentiated, their lacunæ, according to Chun, flow together two by two into a common cavity; and the place of the original four sacs is thus taken by two, from which all the vessels originate by a process of outbulging. My own observations, on the other hand (see above, p. 91), lead me to conclude that the two endodermal sacs which lie one on each of the broad sides of the compressed stomach, become directly transformed into the two deep-lying or gastric vessels, while the remaining two sacs, by lateral extension and dichotomous division, give origin to the rest of the vascular system.

In connexion with the embryology of the Ctenophora, Chun records an observation of considerable interest. He noticed, after a succession of very hot days, that the greater number of larvæ of *Eucharis multicornis* collected by the towing-net had their subventral meridional vessels changed into pouch-like swellings of a whitish colour. Many of these larvæ had plainly only just left the egg, while all were in a very early stage of development. In none of the more advanced larvæ could he find a trace of this peculiar condition of the vessels.

The microscope showed that the whitish pouches were filled with sexual products—that they represented, in fact, hermaphrodite glands, in which occurred, along with sperm-masses, eggs in various stages of development. Chun further proved that the eggs thus produced by the sexually mature larva of *Eucharis* were capable of passing through a development entirely similar to that of the eggs of the adult Ctenophore, from which these differed only in being about half their size; and he concludes that the young larva of *Eucharis* not only becomes sexually mature, but that it gives birth to a brood which again assumes the form of the larva. Several questions, however, connected with this phenomenon still remain unsolved; and the ultimate destiny of the sexually mature larva, and of the brood to which this gives birth, must await further observations for its determination.